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CLIMATIC GRADIENTS IN THE DISTRIBUTION OF KANSAS LAND SNAILS (MOLLUSCA: GASTROPODA)

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ABSTRACT

The distribution of 64 species of land snails (Mollusca: Gastropoda) across the 105 counties of the State of Kansas was analyzed by principal components analysis to determine the relationship between species occurrence and climatic factors. Significant biotic responses of species assemblages to climatic gradients in precipitation and in annual temperature were discovered. In particular, total species diversity is positively correlated with precipitation (annual or summer alone) across the counties of Kansas, and the distributions of major clusters of gastropod species were correlated with average annual temperature (or latitude).

Introduction

This paper presents an analysis of the relationships between the distribution of species assemblages of land snails (Mollusca: Gastropoda) across the counties of the State of Kansas and gradients of climatic variables across those counties. For the large, mid-continental state of Kansas in the years represented by our data, the average annual precipitation across the 105 geopolitical divisions (the counties) ranged from 15.82 to 41.68 inches, while the annual average temperature range was 50.6 to 58.9 °F, and the average number of frost-free days varied between 154 and 198.

Because the State of Kansas shows pronounced geographic clines in climatic conditions, our aim was to explore whether there is a faunal response to these gradients in a group of organisms likely to be dependent upon climatic factors. In a similar geographic study, Kadmon and Heller (1998) found a strong correlation between species distributions of land snails in Israel and the climatic gradients found there.

Materials and Methods

The most recent published survey of species of land snails in Kansas remains the monograph of Leonard (1959), which gives distribution maps for each snail species in the counties of the state. Table 1 lists the 64 gastropod taxa found in Kansas, using nomenclature updated according to the systematic treatment of Turgeon et al. (1988) and earlier works (Pilsbry, 1948; Taylor, 1960; Taylor, 1965). The distribution maps were converted into a presence/absence data table, where each of the 105 counties was scored according to whether each of the species was recorded as present. The counties of Kansas were coded according to a letter-and-number checkerboard scheme (Figure 1), with lower letters of the alphabet to the east and higher numbers to the north. Thus, the most southeastern county (Cherokee) was coded A1, and the most northwestern county (Cheyenne) was coded O8.

Climatic data for the sample localities were taken from the nearest reporting station of the United States Weather Bureau for the period 1899–1938, corresponding to the majority of the collection dates for the specimens collected by Leonard (1959) for the Museum of Natural History at the University of Kansas. The five climatic parameters that were used correspond to average values for the main weather station in each county, using published maps (Kincer, 1941). Their descriptions are given in Table 2, along with latitude and longitude.

All statistical analyses were performed using the SPLUS 2000 software package (MathSoft, 1999). We used principal components analysis (Morrison, 1967; Gauch, 1982) to reduce the complexity of the distributions of the 64 species across the 105 counties in Kansas. This technique is commonly used in analyses of geographic distributions of biotic assemblages (Kadmon and Heller, 1998) to reduce the multivariate dimensionality of the original data. It constructs linear combinations of the original variables (in this case, the presences and absences of 64 species) that maximally encompass the variation in the original data. In particular, the first principal component accounts for the greatest variance in the species data; the second component is perpendicular to and uncorrelated with the first component, and it accounts for the second largest amount of variation; the third component is orthogonal to the first two and accounts for the next largest amount of variation; etc. These synthetic variables thus represent uncorrelated aspects of species distributions across the counties of Kansas.

The principal components for species distribution then were related to latitude, longitude, and the five specific climatic variables for the 105 counties by using simple linear regression and correlation techniques (Gauch, 1982; Sokal & Rohlf, 1995).

Results and Discussion

Principal components analysis of distributions of 64 gastropod species

Principal components analysis of the distributional data, based on the matrix of correlations among the 64 species variates, was successful in capturing a significant fraction of

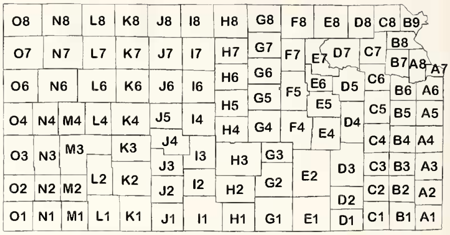

Figure 1. Map of the counties of Kansas, along with their letter-and-number codes, as follows: A1, Cherokee; A2, Crawford; A3, Bourbon; A4, Linn; A5, Miami; A6, Johnson; A7, Wyandotte; A8, Leavenworth; B1, Labette; B2, Neosho; B3, Allen; B4, Anderson; B5, Franklin; B6, Douglas; B7, Jefferson; B8, Atchison; B9, Doniphan; C1, Montgomery; C2, Wilson; C3, Woodson; C4, Coffey; C5, Osage; C6, Shawnee; C7, Jackson; C8, Brown; D1, Chautauqua; D2, Elk; D3, Greenwood; D4, Lyon; D5, Wabaunsee; D7, Pottawatomie; D8, Nemaha; E1, Cowley; E2, Butler; E4, Chase; E5, Morris; E6, Geary; E7, Riley; E8, Marshall; F4, Marion; F5, Dickinson; F7, Clay; F8, Washington; G1, Sumner; G2, Sedgwick; G3, Harvey; G4, McPherson; G5, Saline; G6, Ottawa; G7, Cloud; G8, Republic; H1, Harper; H2, Kingman; H3, Reno; H4, Rice; H5, Ellsworth; H6, Lincoln; H7, Mitchell; H8, Jewell; I1, Barber; I2, Pratt; I3, Stafford; I4, Barton; I6, Russell; I7, Osborne; I8, Smith; J1, Comanche; J2, Kiowa; J3, Edwards; J4, Pawnee; J5, Rush; J6, Ellis; J7, Rooks; J8, Phillips; K1, Clark; K2, Ford; K3, Hodgeman; K4, Ness; K6, Trego; K7, Graham; K8, Norton; L1, Meade; L2, Gray; L4, Lane; L6, Gove; L7, Sheridan; L8, Decatur; M1, Seward; M2, Haskell; M3, Finney; M4, Scott; N1, Stevens; N2, Grant; N3, Kearny; N4, Wichita; N6, Logan; N7, Thomas; N8, Rawlins; O1, Morton; O2, Stanton; O3, Hamilton; O4, Greeley; O6, Wallace; O7, Sherman; O8, Cheyenne.

the variation among all 105 counties in the first three principal components. Principal component 1, which accounted for 20.8 percent of the total variation in the data, loaded positively on all 64 species, except *Succinea pseudavara*, *Succinea vaginacontorta*, and *Gastrocopta cristata*; in other words, it contrasted the occurrences of these three species against those of the other 61 species, among which the highest loadings were attributed to *Zonitoides arboreus*, *Anguispira alternata*, *Philomycus carolinianus*, *Strobilops labyrinthicus*, *Gastrocopta armifera*, *Gastrocopta contracta*, and *Carychium exile*. The second principal component, accounting for another 11.2 percent of the variation, contrasted 19 species against the other 45. The third component comprised an additional 6.2 percent of the variation and contrasted the distributions of a different set of 30 species

Table 1. Systematics of the gastropod species (or subspecies) found in Kansas. The 28 species subset used in a second analysis described in the text is indicated with **boldface**.

Order	Family	Species
Basommatophora		
	Carychiidae	
		Carychium exiguum (Say, 1822)
		Carychium exile exile I. Lea, 1842
Stylommatophora		
	Bulimulidae	
		Bulimulus dealbatus dealbatus (Say, 1821)
	Cochlicopidae	
		Cochlicopa lubrica lubrica (Miller, 1774)
	Discidae	
		Anguispira alternata alternata (Say, 1816)
	Haplotrematidae	
		Haplotrema concavum (Say, 1821)
	Helicarionidae	
		Euconulus chersinus polygyratus (Say, 1821)
	Helicodiscidae	
		Heliocodiscus eigenmanni eigenmanni (Pilsbry, 1900)
		Heliocodiscus parallelus (Say, 1817)
		Heliocodiscus singleyanus singleyanus (Pilsbry, 1890)
	Philomycidae	
		Philomycus carolinianus (Bosc, 1802)
	Polygyridae	
		Allogona profunda (Say, 1821)
		Euchemotrema leai aliciae (A. Binney, 1841)
		Mesodon clausus (Say, 1821)
		Mesodon inflectus inflectus (Say, 1821)
		Mesodon thyroidus thyroidus (Say, 1816)
		Polygyra dorfeuilliana dorfeuilliana (I. Lea, 1838)
		Polygyra dorfeuilliana sampsoni (I. Lea, 1838)
		Polygyra jacksoni jacksoni (Bland, 1866)
		Stenotrema hirsutum hirsutum (Say, 1817)
		Stenotrema stenotrema (Pfeiffer, 1842)
		Triodopsis albolabris alleni (Say, 1816)
		Triodopsis cragini Call, 1886
		Triodopsis divesta (Gould, 1848)
		Triodopsis multilineata algonquinensis (Say, 1821)
		Triodopsis multilineata multilineata (Say, 1821)
		Triodopsis neglecta (Pilsbry, 1899)
	Punctidae	
		Punctum minutissimum (I. Lea, 1841)
	Pupillidae	
		Gastrocopta armifera (Say, 1821)
		Gastrocopta contracta (Say, 1822)
		Gastrocopta corticaria (Say, 1816)
		Gastrocopta cristata (Pilsbry & Vanatta, 1900)
		Gastrocopta holzingeri (Sterki, 1889)
		Gastrocopta pellucida hordeacella (Pfeiffer, 1841)
		Gastrocopta pentodon (Say, 1821)
		Gastrocopta procera procera (Gould, 1840)
		Gastrocopta tappaniana (C. B. Adams, 1842)
		Pupoides albilabris (C. B. Adams, 1841)
		Pupoides hordaceus (Gabb, 1866)
		Pupoides inornatus Vanatta, 1915
		Vertigo milium (Gould, 1840)
		Vertigo ovata ovata Say, 1822
		Vertigo tridentata Wolf, 1870
	Succineidae	
		Catinella vagans (Pilsbry, 1900)
		Catinella wandae (Webb, 1953)
		Oxyloma retusum (I. Lea, 1834)
		Succinea concordialis Gould, 1848
		Succinea ovalis Say, 1817
		Succinea pseudavara Webb, 1954
		Succinea vagiuacontorta Lee, 1951
	Strobilopsidae	
		Strobilops labyrinthicus (Say, 1817)
	Vitrinidae	
		Deroceras laeve (Müller, 1774)
	Zonitidae	
		Hawaiia minuscula minuscula (A. Binney, 1840)
		Mesomphix cupreus ozarkensis (Rafinesque, 1831)
		Nesovitrea electrina (Gould, 1841)
		Nesovitrea identata identata (Say, 1823)
		Paravitrea capsella capsella (Gould, 1851)
		Paravitrea significans (Bland, 1866)
		Paravitrea simpsoni (Pilsbry, 1889)
		Striatura meridionalis (Pilsbry & Ferriss, 1906)
		Striatura milium (E. S. Morse, 1859)
		Ventridens ligera (Say, 1821)
		Zonitoides arboreus (Say, 1816)
	Valloniidae	
		Vallonia parvula Sterki, 1893

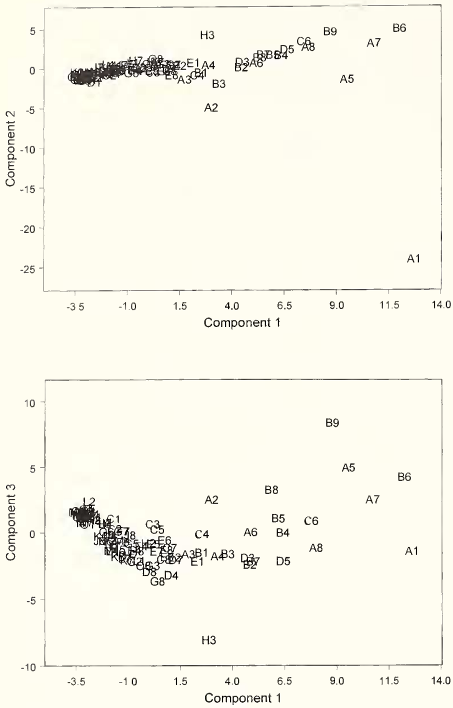

Figure 2. Location of the counties of Kansas (indicated with the locality codes of Figure 1) in the space defined by the first three principal components based on the distribution of 64 gastropod species.

against the remaining 34. Thus, the first three principal components together account for 38 percent of the variation in the distributional data of 64 gastropod species across the 105 counties of Kansas.

Inspection of the location of the individual counties in the three most important dimensions of principal components space (Figure 2) reveals that the most eastern counties of Kansas (codes A1 to D8) occur at the high end of the first principal component, that the most southeastern county (A1: Cherokee) is distinct with respect to the second principal component, and that there is some separation of the eastern counties, as well as H3 (Reno County) along the third component. The superposition of nearly all of the western counties indicate that they are distinct with respect to gastropod assemblages.

Table 2. The seven climatic variables and correlations of the first three principal components (comps.) of species distributions of 64 gastropod species with these climatic variables. The last five variables represent annual averages.

	Comp. 1	Comp. 2	Comp. 3
Latitude (°N)	0.151	0.303	-0.115
Longitude (°W)	-0.730	-0.040	0.099
Annual precipitation (inches)	0.730	0.010	-0.132
Summer precipitation (inches)	0.721	0.034	-0.150
Annual temperature (°F)	0.125	-0.203	-0.023
July temperature (°F)	-0.128	-0.091	-0.040
Number of frost-free days	0.436	0.157	0.013

Table 3. Correlations between principal component (comp.) scores based on 28 gastropod species and climatic variables in the counties of Kansas.

Species	Comp. 1	Comp. 2	Comp. 3
Euchemotrema leai aliciae	0.241	-0.136	0.001
Mesodon thyroidus thyroidus	0.139	-0.009	-0.332
Mesodon clausus	0.163	0.202	0.092
Triodopsis albolabris alleni	0.219	0.213	-0.073
Bulimulus dealbatus dealbatus	0.170	-0.122	-0.104
Euconulus chersinus polygyratus	0.230	0.011	-0.097
Nesovitrea electrina	0.244	0.136	-0.048
Nesovitrea identata identata	0.249	-0.033	-0.085
Paravitrea significans	0.082	-0.030	-0.321
Hawaiia minuscula minuscula	0.179	-0.180	0.166
Striatura milium	0.091	0.385	0.351
Striatura meridionalis	0.091	0.386	0.350
Zonitoides arboreus	0.247	-0.108	-0.011
Anguispira alternata alternata	0.258	0.061	-0.130
Heliocodiscus parallelus	0.180	-0.236	0.149
Punctum minutissimum	0.167	0.238	0.053
Philomycus carolinianus	0.204	0.028	-0.266
Succinea concordialis	0.110	0.141	0.161
Catinella vagans	0.070	0.186	0.169
Strobilops labyrinthicus	0.254	0.102	-0.195
Gastrocopta armifera	0.188	-0.254	0.199
Gastrocopta contracta	0.244	-0.113	-0.009
Gastrocopta pentodon	0.189	0.099	-0.174
Gastrocopta tappaniana	0.160	-0.089	0.066
Gastrocopta procera procera	0.151	-0.222	0.262
Pupoides albilabris	0.167	-0.230	0.199
Vallonia parvula	0.157	-0.282	0.286
Carychium exile exile	0.214	0.247	-0.013

Relationships between species distributions and climatic gradients

Table 2 gives the correlations between the first three principal components and the values for each of the seven climatic factors for each county. It is clear, for example, that the first component is strongly positively correlated with total precipitation ($r = 0.730$, $P < 0.001$) and with summer precipitation ($r = 0.721$, $P < 0.001$), but strongly negatively correlated with longitude ($r = 0.730$, $P < 0.001$). As might be expected from the mid-continental location of Kansas, there is a strong positive correlation between annual and summer precipitation ($r = 0.997$, $P < 0.001$). Furthermore, this state partly was chosen for this study because of the strong relationship ($r = 0.981$, $P < 0.001$) between longitude and precipitation, with a remarkably linear gradient from the wetter east to the drier west (see Figure 3). However, Figure 4 demonstrates that annual precipitation is a good predictor of the first principal component only for the eastern counties, where there generally is a higher diversity of gastropod species (Figure 5). A much better predictor of the first component ($r = 0.976$, $P < 0.001$) is simply the species diversity (Figure 6), although as noted above not all species load positively on this component. Furthermore, the superposition of many of the western counties along the first component that was evident before can be explained, in large part, by their depauperate gastropod populations.

The second principal component is most strongly positively correlated with latitude ($r = 0.303$, $P < 0.01$) and negatively correlated ($r = 0.203$, $P < 0.01$) with annual temperature (Table 2). Since higher latitudes generally correspond with lower temperatures over the counties of Kansas ($r = 0.800$, $P < 0.001$), these relationships imply that the second most important axis of gastropod species distribution can be explained partially by a second, less pronounced climatic gradient. The third principal component correlates only weakly with climatic variables; the highest correlation is with summer precipitation, but it is not statistically significant ($r = 0.150$, $P > 0.05$).

Principal components analysis of distributions of 28 selected gastropod species

In order to test the robustness of these results, a second principal component analysis was undertaken using a subset consisting of 28 of the 64 gastropod species found in Kansas. Table 1 indicates in boldface type the species selected for this analysis, which represent most of the families of gastropods. They include most of the species that loaded highly in the analysis of the full dataset, as listed above. Figure 7 shows the disposition of the 105 counties in the space defined by the first two principal components. Again, a longitudinal trend is evident (with most of the western counties superimposed), plus the separation of B4 (Anderson County) along the second component.

The first principal component in this case loaded positively on all 28 species (see Table 3), with the highest contributions provided by *Anguispira alternata*, *Strobilops labyrinthicus*, *Nesovitrea indentata*, *Zonitoides arboreus*, *Nesovitrea electrina*, *Gastrocopta contracta*, and *Euchemotrema leai*. Many of these same species contributed highly to the first component of the full 64-species dataset. Once again, scores on the first component across the counties of Kansas were highly positively correlated with the climatic factors of annual precipitation ($r =$

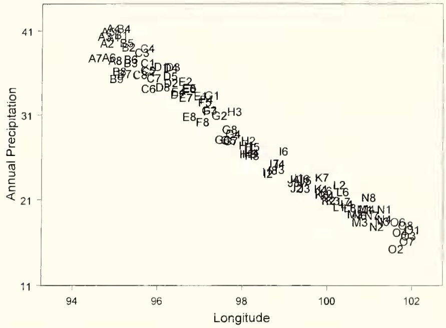

Figure 3. Relationship between longitude and total annual precipitation in Kansas.

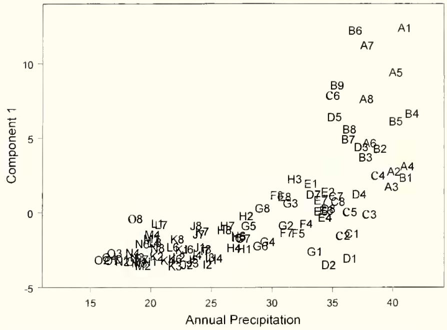

Figure 4. Relationship between total annual precipitation and scores on the first principal component of gastropod species distributions in Kansas.

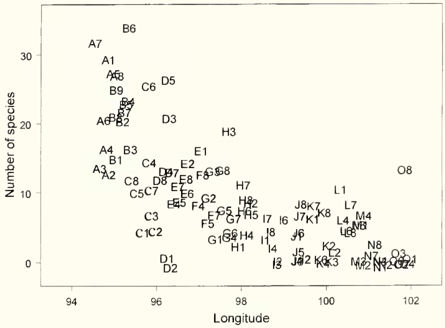

Figure 5. Relationship between longitude and gastropod species diversity in Kansas.

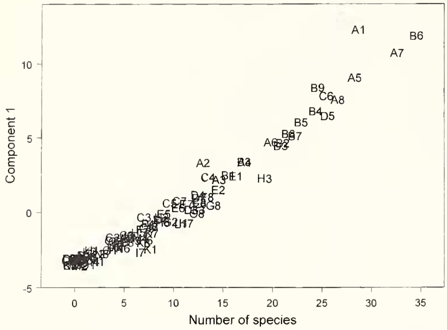

Figure 6. Relationship between gastropod species diversity and the first principal component.

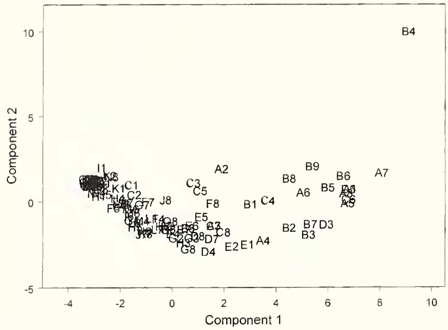

Figure 7. Location of the counties of Kansas in the space defined by the first two principal components based on the distribution of 28 gastropod species.

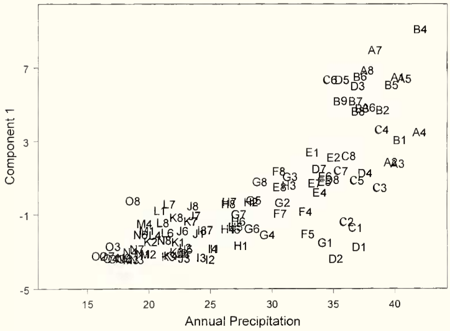

Figure 8. Relationship between total annual precipitation and scores on the first principal component of 28 gastropod species distributions in Kansas.

0.784, $P < 0.001$; Figure 8) and summer precipitation ($r = 0.781$, $P < 0.001$), were highly negatively correlated with longitude ($r = 0.773$, $P < 0.001$), and were very strongly correlated with species diversity ($r = 0.966$, $P < 0.001$).

The second principal component most strongly contrasted the distributions of *Striatura meridionalis*, *Striatura milium*, *Carychium exile*, and *Punctum minutissimum* with those of *Vallonia parvula*, *Gastrocopta armifera*, *Helicodiscus parallelus*, and *Pupoides albilabris*. This component was significantly correlated only with latitude ($r = 0.238$, $P < 0.05$). The third component contrasted the distributions of *Striatura meridionalis*, *Striatura milium*, *Vallonia parvula*, and *Gastrocopta procera* with those of *Mesodon thyroidus*, *Paravitrea significans*, and *Philomycus carolinianus*. It was correlated significantly only with two climatic variables: positively with latitude ($r = 0.372$, $P < 0.01$) and negatively with average temperature ($r = 0.231$, $P < 0.05$); of course, these two variables are correlated negatively with each other, as noted above.

The congruence of the results for the full set of 64 gastropod species found in Kansas and the selected subset of 28 species strengthens our interpretation that there has been a significant biotic response of this group of gastropods to climatic gradients in precipitation (from east to west across the checkerboard of Kansan counties) and, less strongly, in annual temperature (from south to north). These conclusions are comparable to the similarly strong response found by Kadmon and Heller (1998) of the land snails of Israel to a strong rainfall gradient from north to south. To our knowledge, the present study represents the first analysis of the relationship between land snail distributions and climatic factors in the central region of the United States.

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